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ON

CEREBRAL ANATOMY.

An Address delivered at the opening of the Section of Anatomy and Physiology, at the Annual Meeting of the British Medical Association, held in Birmingham, July, 1890.

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ON CEREBRAL ANATOMY.

Ontogeny and Phylogeny.—The Relation of Convolution to Body Weight. —Homogenetic and Homoplastic Agreements.— The Early Development of the Primate Brain.—The Brain of the Ape and of Man.—Annectant Gyri.—The Development of the Principle Fissures.—The Influences which Produce the Fissures and Convolutions.—The Blood Vessel Theory.—The Influence of "Pulsatory Concussions."—The Influence of the Form of the Head. —The Influence of Varying Rates of Growth.—Jelgersma's Theory.

Before entering upon the subject-matter of my address, I think that it would be only right to congratulate Professor Windle and Professor Allen on having organised a Section of Anatomy and Physiology in connection with this meeting of the British Medical Association in Birmingham. The last few years have been unquestionably a time of marked activity in the domain of both of these subjects. Prior to the foundation of the Anatomical Society, a certain amount of lethargy had crept over anatomists. Individual work and good work was no doubt done, but there was no cohesion—no combined effort.

The Section which we now open I regard as an expression of this renewed activity; and I am glad that physiology is associated with anatomy. Notwithstanding the many new and important developments of physiology, bringing it into close touch, on the one hand, with chemistry, and, on the other hand, with physics, the link which binds it to anatomy is not thereby lessened in its strength, and it must always be profitable for the workers in the two fields to meet on the same platform, and to discuss the problems which are engaging their thoughts from the functional as well as from the morphological standpoint.

I have selected as the subject of my address the field in which I have been most recently occupied, and to which my thoughts have been chiefly directed for the last two or three years. I refer to the fissures and convolutions of the cerebral hemispheres. It is, indeed, strange that this ground, apparently so limited and circumscribed, should still be capable of yielding rich results to anyone who devotes himself earnestly to the work. But such is, indeed, the case, notwithstanding the great advance that has been made in cerebral anatomy during the present century, and more especially during the last forty-five years.

It is true that we no longer look upon the cerebral convolutions as being disposed in an unmeaning disorder; we no longer compare them to the coils of the small intestine. The labours of

Leuret, Gratiolet, and Broca in France, Huschka, Bischoff, and Ecker, in Germany, and Huxley, Turner, and Flower in this country have taken us many stages beyond this. The descriptive anatomy of the human cerebrum is now very nearly complete; what still remains to be done is the establishment of our knowledge upon a proper morphological basis.

In approaching the subject from the phylogenetic side, there is an overwhelming amount of material ready to hand. The brain of the ape is nearly as well known as that of man, and it has likewise been studied with an equal amount of care in almost every animal group.

Further, the facts acquired in this manner have been compared and checked by the evidence afforded by ontogeny, or by the study of the developing brain. It must be admitted, however, that in the case of the primate brain this evidence is somewhat one-sided. Little or nothing is known of the manner in which the fissures and convolutions appear in the fœtal ape. In so far as the human brain is concerned, the material is very abundant, but the picture afforded is so variable, that very different interpretations may be arrived at by different observers. Certainly it cannot be too strongly insisted on that it is only from large numbers of developing brains in each stage of growth that correct and trustworthy information can be gathered; and seeing that the development of the permanent fissures is compressed into the last four months of intrauterine growth, there should be little difficulty in meeting this requirement.

The law that ontogeny is a brief recapitulation of phylogeny, or, in other words, that the germ-development is a compressed and shortened repetition of the stem-development, is a generalisation which is now within certain limits universally admitted, and what is true for the organism as a whole is also true for the various parts which build it up; but when we apply this rule to the study of the cerebral convolutions, we are met with the difficulty that the two lines of evidence in many cases yield us what appear to be contradictory results.

There is a general consensus of opinion amongst anatomists that the fissures and convolutions of the primate brain are arranged according to a pattern which can be compared with the arched fissures and convolutions of the carnivore brain, and yet it must be admitted that the ontogeny of the human brain affords us no assistance in our endeavours to detect in what particulars the carnivore pattern is repeated in the primate cerebrum. The ontogenetic and phylogenetic evidence are apparently at variance with each other; the whole chapter before the primate stage (if, indeed, such a chapter ever existed) is as it were entirely effaced, or at least so blurred and shortened, that it is impossible to recognise the any trace of it. Where, for instance, can we perceive the least degree of resemblance between the three radial "Primärfurche" of Bischoff and Pansch, so conspicuous in the human fœtal brain, and the convolution type of the carnivora? Indeed, it is in the adult brain, and not in the fœtal brain, that what correspondence there is can be most easily followed.

But are we sure that the phylogenetic chapter which we expect to be repeated in the ontogeny of the primate brain had ever really any existence? Are we right in trying to compare all convoluted brains with each other, seeing that an increase in the body weight of an animal produces a stronger development of the furrows and convolutions without necessarily giving rise to a higher brain organisation? In some of the smaller forms of apes, for example, the brains are smooth, and yet on account of this we

do not give them a lower place in the organic scale. Further, before we seek to detect homologies between the furrows and convolutions of two different animals, should we not in the first instance hold it as an essential that the animals under consideration be descended from a stem-form or common ancestor with a more or less convoluted brain? But this is not the case with the primates and the carnivora. These two groups have in all probability been derived from a stem-form with a smooth brain, and the furrows and convolutions in the brain of each are the product of an after-development. Might we not fairly ask whether the different convolution type in each is not the result of this? Jelgersma, of Meerenberg,[1] has recently advocated these views with great ability, and there cannot be a doubt but that a great deal can be said in support of them.

It appears to me, however, that the physiologist will have something to say on the other side. In a smooth cerebrum the same leading functional areas are doubtless present as in a convoluted cerebrum, and, although similarity of function is altogether inadmissible as a factor to be considered in the determination of

Fig. 1.—Outer surface of a cerebrum of a fœtus between the third and fourth month of development. The transitory infoldings are well marked. All these disappear at a subsequent stage of growth and the cerebral surface becomes smooth.

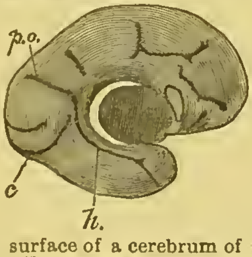

Fig. 2.—Inner or mesial surface of a cerebrum of a fœtus in the early part of the fourth month. Transitory infoldings and the complete permanent fissures are seen. *h*. Hippocampal fissure; *c*, calcarine fissure; *p.o*, parieto-occipital fissure.

homologies, it is not unlikely that these areas are really in a certain sense homologous in both. Later on, when I come to speak of the influences at work in producing the convolutions, I shall endeavour to show that they probably take origin by the outgrowth of areas of functional activity. If this be the case, there is every likelihood of a somewhat similar surface pattern of the brain being produced, even in animals whose only connection lies in a smooth-brained ancestor. Such convolutions and fissures cannot be regarded as homogenetic, because they have no genetic relation; but Professor Ray Lankester[2] has suggested a term which meets the requirements of the case. I refer to the word homoplastic, which "includes all cases of close resemblance of form

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[1] *Morphologisches Jahrbuch*, June, 1889.

[2] "On the Use of the term Homology in Modern Zoology, and the Distinction between Homogenetic and Homoplastic Agreements, *Annals and Magazine of Natural History*, 1870.

which are not traceable to homogeny, all details of agreement not homogenous, in structures which are broadly homogenous, as well as in structures having no genetic affinity."

About the third month in the development of the primate brain, when the cerebral wall is little thicker than the skull capsule which encloses it, a rich series of transitory fissures make their appearance. In six weeks these furrows, with two, or it may be three, exceptions, are completely obliterated, and the cerebral surface again becomes smooth preparatory to the formation of the permanent sulci. For a short time I thought that it might be possible to establish a connection between these temporary fissures and the convolution type of the lower mammals, but in this I was completely deceived. They have an altogether different significance, and in all probability they are peculiar to the primate brain, in which they mark a distinctive and curious stage of growth.[3]

But to pass from the lower mammals, and to confine our attention to the primates, let us consider how far the convolution type of the ape's brain corresponds with that of man, and how far the differences which exist can be cleared up by the light which is thrown on the question by ontogeny.

Putting aside the great advance in the development of the lower part of the frontal lobe in the human brain, a development which leads to the complete formation of the speech centre, we find that all the principal fissures and convolutions in the primate brain show a more or less precise homology with each other. The differences which do exist are of a twofold nature—namely, (1) a greater richness of secondary furrows and convolutions in man, and (2) a marked tendency in the human cerebrum towards the breaking up of the principal fissures into two or more component parts by the formation of deep or superficial annectant gyri.

The secondary furrows of the human brain do not make their appearance until the last month of intrauterine development, and are only completed in the first month of infancy. This would seem to indicate that they are, comparatively speaking, a recent acquisition by the stem-form.

The disruption of the principal fissures, however, by annectant gyri shows itself in the earliest stages of the development of these sulci, and is therefore to be regarded as a deep-seated and important distinctive character of the human cerebrum. Such being the case, I may be allowed to develop this aspect of the subject a little more fully, and for this purpose we shall choose as examples two of the radial "Primärfurche," namely, the fissure of Rolando and the intraparietal sulcus of Turner.

If the lips of the fissure of Rolando be widely separated from each other a distinct deep annectant gyrus will in many cases be observed to cross its bottom, and thus partially cut off its upper third. In certain rare instances this gyrus has been observed to come to the surface and completely break up the fissure of Rolando into two portions. Such a condition, for example, was present in the cerebrum of the celebrated physician Fuchs. In no ape, with the exception of the chimpanzee, and to a less extent the ourang, can this deep annectant gyrus be seen.[4]

But the intraparietal sulcus affords us a more striking example of the disruption of a primary fissure. In the ape this is a long continuous sharply-cut fissure, whilst in man it is broken up into

[3] "The Complete Fissures of the Human Cerebrum and their Significance in Connection with the Growth of the Hemisphere." By D. J. Cunningham. *Journ. Anat. and Phys.*, vol. xxiv.

[4] I have not had an opportunity of studying the brain of the gorilla.

two, three, or even four pieces by the development of deep, or in many cases superficial, gyri.

Wernicke[5] held that these deep annectant gyri were peculiar to man, but this is not the case. Even in the baboon I have noticed one in the bottom of the intraparietal sulcus at the point where in man the ramus occipitalis becomes cut off; and in the chimpanzee one or even two are not infrequently found in the same fissure at points similar to those in which they are developed in the human brain.

I have said that this is a deep-rooted distinction between man and the man-like apes on the one hand, and the lower apes on the other hand, and one which is not bridged over by the condition present in the fœtus. But upon this point it is impossible to speak too cautiously. As I have mentioned, we have little or no information regarding the manner of appearance of the fissures in the fœtal ape, and it is naturally in the earlier conditions of the two forms that we would expect the greater degree of approximation. Still, anyone who studies closely the material at present at our disposal must come to the conclusion that the difference between the human and the ape brain, in so far as the primary fissures are concerned, is distinctly emphasised in the fœtal condition, or, in other words, that the developing human brain is further removed in this respect from the ape type than that of the adult.

The more usual mode of development of the principal fissures of the human brain, and more particularly the intraparietal, is not in the form of a long continuous groove, or a groove which lengthens out from one or other or both ends, and in the bottom of which annectant gyri make their appearance later on, but in the form of distinct and isolated pieces. Indeed, it is not infrequent for the two most distant parts of a fissure to show first, and for the intermediate portions to develop later. All this has a most important bearing upon the development of the annectant gyri, which are so distinctive of the higher brain organisation. The bridges of brain cortex which intervene between the isolated portions of a developing fissure are ultimately borne down as the pieces run into each other; but they are not, as a rule, completely obliterated. In the bottom of the fissure they still show as deep annectant gyri. In some cases, indeed, they prove an efficient barrier to the junction of two adjacent portions of a developing fissure, and then they form superficial gyri.

I do not say that this is the way in which these interrupting gyri invariably arise, although I believe it to be the chief and most important mode of development.

It is a dangerous thing to draw conclusions regarding development from the condition present in the adult; still I cannot help entertaining the idea that were the ontogeny of the ape's brain known, we should find in the chimpanzee and orang, and probably also in the gorilla, a tendency exhibited towards the interrupted or human mode of development, whilst amongst the lower apes the continuous method would hold good. The straight continuous fissures of the latter, with their smooth walls and uniform depth, all point to this.

The development of the fissure of Rolando offers some points of considerable interest and importance. In many cases it arises, no doubt as is usually described, in the form of a continuous groove, which is steadily deepened by the upheaval of its bounding banks. But very frequently it takes origin in two portions. Of these the

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[5] "Das Urwindungs-system des menschlichen Gehirns," *Archiv für Psychiatrie* Band vi, Heft I, 1875.

lower and the longer part makes its appearance first as a continuous groove. The upper part has an independent origin. It first shows as a slight depression, which widens and deepens and is separated from the lower part of the furrow by a high bridge of cortex. A faint groove then runs over the surface of this bridge, and connects the two parts. In course of time the bridge disappears from the surface as the connecting groove cuts deeper and deeper into it, but in the after-growth of the brain it is retained in the form of the annectant gyrus to which I have referred.

This does not coincide with the account which is given by Krause[6] of the development of the fissure of Rolando. This author holds that it is caused by a constricting vein, which stretches from the superior longitudinal sinus to the Sylvian fossa, and cuts into the cerebral surface. If this were the case it would be impossible for the fissure to appear in two detached portions. In all cases the middle or most projecting part of the convex surface of the cerebrum would be affected first, and from this the furrow would extend uniformly upwards and downwards.

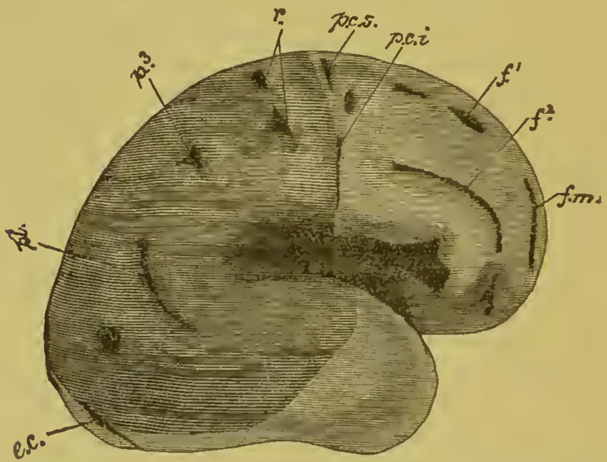

Fig. 3.—Cerebral hemisphere in the early part of the sixth month of development. The interrupted mode of fissural formation is well seen. *r*, two parts of the fissure of Rolando; *p c i*, sulcus præcentralis superior; f^1, sulcus frontalis superior; f^2, sulcus frontalis inferior: *fm*, sulcus frontalis medlus (See Eberstaller's *Das Stirnhirn*); p^3 ramus horizontalis (of the intraperitoneal); *p l*, parallel sulcus; *e c*, external calcarine.

I might pursue this aspect of the question further, but it is needless to do so. I have pointed out elsewhere in the parieto-occipital and calcarine fissures an apparent contradiction in the phylogenetic and ontogenetic evidence,[7] but in all cases it is necessary not to lose sight of the fact that if we had the developing brain of the ape before us such difficulties and discrepancies would, no doubt, in most cases melt away, and differences would be reconciled.

But I have set myself another task in this address, and that is to discuss the influences at work in producing the furrows and convolutions on the surface of the cerebrum. Many theories have

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6 *Handbuch der menschlichen Anatomie*, Zweiter Band, p. 813.

7 "The Complete Fissures of the Human Cerebrum, etc., *Journal of Anat. and Phys.*, vol. xxiv.

been advanced to account for these. By some observers they have been regarded as being due to the influence of mechanical forces operating on the brain from without; by others they have been considered to be the effect of different degrees of growth tension acting on the surface of the cerebrum from within.

Two widely different forces have been thought to exercise a mechanical influence upon the surface of the growing cerebrum, namely, the blood vessels and the enclosing skull capsule. But the advocates of these views are by no means agreed as to the precise manner in which the external influence is applied.

It has been my experience that most anatomists, in reflecting upon this question, are in the first instance attracted by the "blood-vessel" theory, but as they enter more deeply into the study of cerebral growth, they find that it has no solid basis of support. Further, there appears to be a prevalent belief that Reichert was the leading exponent of this view, but anyone who reads his remarkable book upon *The Structure of the Human Brain*,[8] will see that this is not the case. He calls attention it is true to the striking agreement which exists between the type of branching of the cerebral arteries and the arrangement of the furrows and convolutions. He leads one to infer that the radial sulci of the island of Reil are caused by the pressure of the branches of the middle cerebral artery, but he nowhere distinctly commits himself to this opinion. Indeed he states that the convolutions are chiefly formed by the growth energy of penetrating processes of the vascular pia mater. In the blood supply of the brain it is an absolute necessity that the blood vessels which enter should be exceedingly fine, and this requires a corresponding increase in the extent of the surface. Johann Seitz,[9] who in the main follows Reichert, applies to the fissures of the cerebrum the name of "Nährschlitzë" or nutritive slits.

So far as I am aware, there is no anatomist who maintains that the entire fissural system is the result of the pressure exercised by blood vessels on the surface of the growing cerebrum. Mihalkovics[10] considers that the larger blood vessels must have some influence upon the formation of the cortical furrows, and Krause,[11] who entertains a similar view, specially singles out the fissure of Rolando, the calloso-marginal, and several of the secondary sulci as being produced in this way, while he even hints at a similar origin for the parieto-occipital and calcarine fissures.

It is true that there is a general correspondence to be noted between the course of the blood vessels and the fissures of the cerebrum, but the former have absolutely nothing to do in determining the existence of the latter. Were this the case, the largest vessels would always occupy the deepest furrows, and in all cases they would lie at the bottom of the furrows. As we very well know, however, neither of these conditions is present. Again, if we follow the branches of the middle cerebral artery we perceive that they are placed sometimes between the lips of a fissure, whilst at other times they pass across the surface of the convolutions. But, as Schwalbe has pointed out, the strongest argument against the theory is to be found in the cerebellum. There cannot be a doubt that the same causes which are responsible for the production of the cerebral sulci must also be responsible for the formation of the cerebellar fissures, and yet, in the case of the

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[8] *Der Bau des menschlichen Gehirns*, Leipzig, 1861.
[9] *Ueber die Bedeutung der Hirnfurchung*, Leipzig und Wien, 1887.
[10] *Entwicklungsgeschichte des Gehirns*, p. 151. Leipzig. 1887.
[11] *Handbuch der menschlichen Anatomie*, Zweiter Band, p. 813. Hannover. 1879.

cerebellum, the larger vessels do not occupy the fissures, but are placed on the surface of the organ.

But have we no markings on the surface of the cerebrum which are due to vascular pressure? Certainly we have, but not in the shape of fissures. If a brain be carefully hardened *in situ*, or if it be successfully removed when perfectly fresh, and at once plunged into a chloride of zinc bath, a deep wide groove will usually be observed curving downwards and outwards over the occipital pole of the right hemisphere. The right lateral sinus is responsible for this impression, and the forked posterior extremity of the calcarine fissure occupies the bottom of the groove. Again, if the blood vessels have been injected beforehand it will be seen that where they cross the surface of a convolution their course is marked by shallow but sharply cut grooves. Another example is to be found in the so-called præoccipital notch which indents the lower border of the hemisphere and marks the anterior limit of the occipital lobe below. Schwalbe would seem to indicate that this notch is the representative of the fissura præoccipitalis of Meynert in the ape's brain. It is true that the bottom of the notch is often traversed by a fissure, but this is merely related to it in the same way that the extremity of the calcarine fissure is related to the lateral sinus groove on the occipital pole of the cerebral hemisphere.

The præoccipital notch is formed at a point which very nearly corresponds with the middle of the parieto-mastoid suture. Here three veins, converging towards each other from the outer surface of the hemisphere, open into the lateral sinus which lies immediately below the under border of this part of the cerebrum. Tension of these veins produced by cranial growth at the suture line is the usual cause of the præoccipital notch. In many cases, however, where the notch is strongly marked, another factor comes into play. Immediately behind is the asterion—the star-like sutural meeting of the occipital, mastoidal, and parietal bones. The attachment of the tentorium with the enclosed lateral sinus crosses the deep surface of the asterion, and the growth of the skull capsule which takes place here as from a centre drags upon the dura mater, and raises it into more or less salient folds. One of these, opposite the middle of the parieto-mastoid suture, is usually more marked than the others, and, cutting deeply into the lower border of the hemisphere, co-operates with the veins already mentioned in producing the notch. Anyone who makes a cast of the interior of the growing cranium of a child, in which the dura mater and the tentorium are undisturbed, can readily prove the truth of my statement.

None of these markings produced on the surface of the cerebrum by blood vessels can be classed as true cerebral sulci, and therefore we dismiss the constricting influence of vessels as being altogether outside the sphere of the causes which operate on the brain in the production of the convolutions.

But quite recently the vascular theory has received a new and important development in a totally different direction at the hands of Dr. Richter,[12] of Dalldorf. This author argues with much ingenuity that the furrows on the surface of the cerebral hemispheres are produced by the movements of the fœtal brain. During the heart systole the passage of the blood into the minute twigs of all the blood vessels causes the brain to swell up from the base of the cranium in a centrifugal direction by squeezing

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[12] "Ueber die Entstehung der Grosshirnwindungen," *Virchow's Archiv*, Berlin, 1887.

out the cerebrospinal fluid from the interior of the ventricles. The borders of the brain are thus pressed into all the recesses of the skull cavity, and the organ receives a concussion which travels in an inward direction upon the surface of the hemispheres. Richter compares this concussion to the waves or ripples which may be generated at the borders of a vessel filled with water. In such a case, however, the waves are raised towards the outer surface, and each draws itself further away, whilst in the case of the brain the influences produced by the molecular concussions of the brain deviate inwards, and along their lines of meeting they become broken and annulled. Richter believes that a disturbance of the surface growth of the cerebrum is the result. He argues that in the stable existence of these interference lines the cells of the ganglionic layer are not all placed in equally favourable circumstances in so far as their growth tendencies are concerned. Those which lie in the lines of interference, or in other words in the lines in which the molecular concussions are broken, will suffer a check to their growth. Through this arrest the furrows arise.

It is impossible to do justice to this theory in the short notice which I am able to give it, but as an illustration I may briefly point out the mannner in which Richter believes the fissure of Rolando to be formed. He regards this fissure as being, as a rule, the "first expression of the collective pulsatory concussions of the lateral surface of the cerebral hemisphere." Its oblique direction is due to the fact that the concussions, which travel along the medial border and which give rise to the upper end of the sulcus, are not interfered with until they reach the parieto-occipital and calcarine infoldings, whilst below they are early called to a halt by the fore part of the Sylvian fossa. Richter asserts that if we were to obliterate the parieto-occipital fissure and the Sylvian depression, the fissure of Rolando would proceed perpendicularly downwards from the mid-point of the medial border of the hemisphere.

The same author further contends that as the hemispheres present a greater antero-posterior than a vertical diameter, the furrows which pursue a sagittal direction must be more numerous than those which run in a coronal direction, and in this manner he explains, without calling in to his aid the influence of the enclosing skull capsule, why it is that in brachycephalic brains the coronal fissural type predominates, whilst in dolichocephalic heads the sagittal fissural type is obvious. Richter's views, therefore, may be briefly stated thus. On the cerebral surface there are different degrees of growth energy. Along the lines of interference or breakage of the pulsatory molecular concussions there is a check to surface growth, and by reason of this furrows are induced. In the areas between these furrows there is an exuberance of growth which leads to the formation of the convolutions.

I shall not pause at this stage to criticise this theory at any length. It is open to an unanswerable objection which affects it in common with all other explanations which represent the fissures and convolutions as the product of mechanical influences operating upon the brain surface. As bearing specially on this view, however, I would urge that if the interference lines of the concussions are so stable as Richter would seem to imply, the various furrows should make their appearance in regular sequence, and always in the same manner. This we know to be very far from the case. There is the greatest variability in the order in which the furrows appear, and in general also they do

not follow a uniform plan of development. The character and the direction of the concussions must, further, to some extent be influenced by variations in the arrangement of the main blood vessels at the base of the brain. Anomalies of this kind are by no means rare, and yet it has never been pointed out that they are associated with any disturbance of the convolutionary type.

Somewhere about the beginning of the third month of development the thin cerebral wall is thrown into a series of deep infoldings involving its entire thickness. These are undoubtedly the result of a want of harmony between the growth of the cerebrum and the enclosing skull capsule. Later on, as the cranial cavity expands, the majority of these deep fissures become unfolded, and the surface of the brain becomes smooth. In this condition it remains until the permanent cortical furrows make their appearance.

Fig. 4.—Section through the frontal region of an early cerebral hemisphere to show the infolding of the wall produced by a transitory fissure, *t. i.*

Now, several observers are of opinion that the permanent furrows owe their origin to the same causes that determine the transitory infoldings and the complete fissures. Henle[13] is chiefly responsible for this view, but it has also been enunciated by Meynert,[14] Meyer,[15] and others. According to these authorities, therefore, the convolutions and furrows are called into existence by a growth antagonism between the brain and and the skull. The cereb al surface grows more rapidly than the cranial cavity within which it is enclosed, and as a natural result of this growth restraint the cerebral surface becomes folded along lines which run at right angles to the axis of the growth energy. Horizontal convolutions would therefore arise in cases where growth is restrained in the vertical direction, and coronal convolutions where it is resisted in the sagittal direction.

Meynert shows that the form of the head in different mammals

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13 *Handbuch der Nervenlehre des Menschen*, 2 Aufl., pp. 177, 183, and 185. Braunschweig. 1879.

14 "Vorlaüfige Mittheilung über die Ursachen des Zustandekommens der Grosshirnwindungen," *Anzeiger der k. k. Gesellschaft der Aertze in Wien*, 1876, No. 29, S. 162 (*Medicinische Jahrbücher*).

15 "Ueber den Einfluss der Schädelform auf die Richtung der Grosshirnwindungen," *Centralblatt für die medicinischen Wissenschaften*, October 21st, 1876, No. 43.

exercises a marked influence upon the direction assumed by the convolutions of the brain. To render this clear, I may be allowed to quote the results which he obtained for the fox, the lion, and the elephant. In the fox the cranial cavity is more elongated than in the others. It presents a cephalic index of 77, and in accordance with this the cerebral fissures run more distinctly in a longitudinal direction than in the lion, which presents a cephalic index of 98.7. The elephant shows a striking degree of hyperbrachycephaly; its cephalic index amounts to 123.3 in the adult animal and 128.3 in the young animal, and in its cerebrum the convolutions and furrows assume an almost vertical direction.

Further, Calori,[16] Meyer, and Rüdinger[17] have called attention to the fact that even in the human brain a relation between the form of the head and the direction of the cerebral furrows may be traced. This is indeed an undoubted fact, and one which can be readily established by anyone who examines the brain *in situ*. The fissure of Rolando lends itself specially to such an investigation. In brachycephalic heads the angle which it forms with the mesial plane opens up, whilst in dolichocephalic heads it becomes more acute. More recently Zuckerkandl[18] has endeavoured to prove that early synostosis produces a change in the arrangement of the furrows, and that not only the skull and its several segments, but also the cranial sutures, have an influence in this direction.

That the initial cause of the formation of the cerebral furrows is to be sought for in a restraint upon the surface growth of the cerebrum, I would deny in the strongest terms. At the time when the first permanent cortical fissures appear, the cerebrum lies loose within the cranial cavity, and does not completely fill it. Ecker[19] pointed this out in his classical memoir upon the development of the cerebral fissures; and it is a fact which I have had many opportunities of verifying. The question as to whether the cranial wall, after the formation of the convolutions, exercises any influence upon their direction is a more difficult one to solve. Is the brachycephalic brain moulded into shape by the brachycephalic skull? or are both the result of the same hereditary influence, and, therefore, in perfect harmony with each other as to their growth? I am inclined to adopt the latter view; and, such being the case, I do not believe that, in normal conditions, the direction of the furrows and convolutions are affected by a restraint placed upon the growth of the cerebrum by the skull capsule. Rüdinger insists strongly that the anatomical peculiarities of brachycephalic and dolichocephalic heads are determined prior to birth.

But certain observers have endeavoured to explain the formation of the cerebral convolutions by influences operating upon the surface of the hemispheres from within. The theory advocated by Wundt[20] is one of the most notable of these. Different intensities of growth in stated directions, leading to surface tension of the cerebrum, is the explanation which he offers.

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16 "Dei cervello nei due tipi brachicephalo e dolicocephalo Italiani, *Memorie dell'Accad. delle Sc. di Bologna*, 2 ser., t. x, Fasc. i, 1871.

17 *Ueber die Unterschiede der Grosshirnwindungen nach den Geschlecht beim Fœtus und Neugeborenen*, München, 1877.

18 "Beweise dass die Nähte auf die Richtung der Windungen Einfluss nehmen," *Wiener medicinische Jahrbücher*, 1883.

19 *Archiv für Anthropologie.* Drittes Band, Drittes und Viertes Heft. 1869.

20 *Grundzüge der physiologischen Psychologie.* 2 Aufl. Leipzig, 1880. 1 Bd. I have not had an opportunity of studying Wundt's views at first hand. An admirable account of the hypothesis is given by Schwalbe in his *Lehrbuch der Neurologie*, p. 576.

To illustrate this view, let us suppose that the smooth surface of the fœtal brain is growing more rapidly in the sagittal than in the transverse direction. Tension of the surface in a transverse direction is thereby induced, and the cerebrum becomes transversely folded in accordance with the direction of strongest tension. Longitudinal furrows, on the other hand, arise if the transverse surface growth outstrips the longitudinal growth, and, as a consequence of this, the surface tension assumes a sagittal direction.

According to Wundt, therefore, the direction of the developing furrows coincides with the direction of the most acute surface tension, or, in other words, stands at right angles to the axis of the greatest growth energy. Schwalbe is not too severe in his criticism of these deductions when he says that they are founded upon no positive proof, and, further, that they are directly contradicted by the fact that in dolichocephalic heads we have a preponderating tendency towards the formation of longitudinal furrows, and in brachycephalic heads a distinct tendency towards the formation of transverse furrows. If Wundt's views were correct, we would expect to find exactly the opposite.

We have now discussed several of the leading theories which have been advanced to explain the initial causation of the cerebral convolutions, and we have noted certain points in each which are open to objection. But further it is impossible to show by means of any of them how it comes about that small animals have smooth brains and large animals convoluted brains; how, in short, we should find in the beaver, an animal remarkable for its intelligence, a cerebrum almost entirely smooth; and in the sheep, an animal—shall we say, remarkable for its dulness—a high convolutionary system. Or, to take a still more striking instance, why in a cetacean we should encounter a cerebrum perfectly bewildering in the complexity of its convolutions and in the little marmoset monkey a brain that is practically without gyri. It was Dareste who first called attention to this striking contrast between the brains of small and large animals, and he showed that it was quite independent of class relationships.

Within the last year Jelgersma[21], of Meerenberg, has developed a theory which appears to meet the difficulty. Not only does it afford a reasonable explanation of the forces at work in calling the convolutions into existence, but the apparent discrepancies in the case of animals of different bulk is made its strongest pedestal of support. The importance and interest attached to Jelgersma's views are such that they are the best excuse I can offer for dealing with them in some detail.

The grey cortex of the brain, which in members of the same species maintains a tolerably constant thickness, increases by surface extension. Further, with every advance in the growth of the grey matter there must be a proportionate increase of the subjacent white matter, the conducting fibres with which it stands in connection. Now if we extend the surface of a smooth-brained animal say four times, and at the same time desire to keep the surface even, we must provide eight times as much white matter to fill the interior of the grey capsule; or, to put it in different terms, if we lengthen out the radius of the cerebrum say ten times, we acquire a surface extension 100 times greater, and an internal capacity 1,000 times greater. The geometrical law involved is simply this—that in the growth of a body the surface

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[21] Ueber den Bau des Säugethiergehirns. *Morphologisches Jahrbuch*, June, 1889.

increases with the second, but the interior with the third, power of the radius.

From this it is evident, seeing that the proportion of internal white matter and external grey matter is in all cases a uniform one, that in the evolution of a large animal out of a small animal a disproportion between the grey capsule and the white core of the cerebrum must result. This is compensated for by the extended cortex placing itself in folds or puckers, and thereby reducing the capacity of the capsule to a degree which brings it into correspondence with the white contents; consequently "the formation of the convolutions and furrows is simply the result of the tendency on the part of the superficial layer to increase by surface extension, and of a mutual space accommodation (*Raum-accommodation*) of the grey substance and of the white conducting paths."

It is but right that I should state—although, indeed, Jelgersma appears to be ignorant of the fact—that many years ago Baillarger arrived at very similar conclusions; and, further, that the theory in question has received independent testimony in its favour at the hands of my colleague, Professor George F. Fitzgerald. Some months ago, having constantly had occasion to appreciate the unsatisfactory nature of the current explanations as to the origin of the convolutions, I detailed to Professor Fitzgerald, as far as I could, the conditions of cerebral growth, and asked if he could account for the presence of the cortical furrows upon geometrical principles. The views which he advanced were identical with those of Baillarger and Jelgersma.[22]

But Jelgersma brings forward some additional facts, which are well worthy of our consideration. He points out that the extent of the cerebral surface depends upon two factors, namely, (1) the absolute quantity of the grey matter, and (2) the thickness with which this is spread over the surface. The absolute quantity of grey matter present is determined by the bulk or by the psychical endowments of the animal, or by both of these factors together. On the other hand, although the thickness of the grey cortex is very much the same in the same species; it differs considerably in different animal groups, and it follows from the theory which he has advanced that the more sparsely the grey substance is spread over the surface of the white matter the richer will be the convolution type. In the cetacean cerebrum the grey cortex is exceedingly thin, and it is due to this that the surface shows such an extreme condition of complexity.

But there is another way of looking at this question, and it is this: Anything which diminishes the quantity of internal white matter will of necessity tend to increase the folding of the external grey capsule; and in a short additional paper, published last March, Jelgersma[23] discusses in this light the effect produced by total or partial suppression of the corpus callosum on the convolutionary type of the cerebrum. The question is a difficult one, because defects in the corpus callosum are very frequently associated with dilatation of the ventricular system, which of course would compensate fully for any deficiency in the white central core of the hemisphere.

A profound convolutionary disturbance accompanies the non-

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[22] I am also informed by Mr. John Marshall, F.R.S., that the same doctrine was taught by Dr. Sharpey in University College, London.

[23] "Das Gehirn ohne Balken: ein Beitrag zur Windungstheorie," *Neurologisches Centralblatt*, March, 1890.

development of the corpus callosum. In a recent paper[24] I have shown that there appears to be present in such cases a marked tendency towards the retention of certain of the primitive transitory fissures, and sometimes also there is in addition an intricacy of pattern produced which presents a superficial resemblance to that seen in the cetacean cerebrum. Hans Virchow[25] has figured and described a brain of this kind.

The same law by which we account for the formation of the cerebral convolutions likewise explains the development of the cerebellar folia. Jelgersma is wrong, however, when he states that no one prior to himself has attempted to place the cerebellar and cerebral convolutions on the same footing. Kölliker[26] distinctly rejects certain theories which have been applied to the cerebrum because they will not suit the cerebellum, and Schwalbe[27] indirectly does the same. The enormous extension of the cerebellar surface by its complicated subdivision into folia is due to the thinness of the grey cortex, and more especially—as, indeed, Jelgersma has pointed out—to the fact that the most important constituents of this layer, the antlered cells of Purkinje, are arranged in a single row. Still further, the wavy crenated outline of the corpora dentata of the cerebellum and the olivary bodies is produced by the same cause, namely, an extension of the grey capsule and an accommodation of this to its contents by a puckering of its walls.

Jelgersma confesses that he is unable to explain why the furrows and convolutions of the cerebrum, always within certain limits, assume a corresponding arrangement in different members of the animal group. It appears to me, however, that if the theory of cerebral localisation be true, the cortex must grow in accordance with the functional activity which is displayed in its different parts. It is true that these functional areas overlap each other to a considerable extent, but districts of especial functional intensity can always be detected. In its growth, therefore, the surface extension of the cerebrum cannot be uniform. In all probability the bulgings out in the form of convolutions are connected with the functions which the areas involved have to perform. It is absolutely necessary that the areas so extended should assume the form of outward puckerings unless an undue quantity of white matter grows all over the inside, and this, of course, is an impossibility.

It may be said that the explanation which we have given is merely another way of stating what has so often been urged in regard to the surface of the brain, namely, that the furrows are produced by linear arrests of growth, and that the convolutions are formed by exuberant growth in the intervening districts. In a certain sense this is perfectly true, but I think that it will be admitted that two very essential points are added. In the first place a reason has been given which indicates the influences at work in determining the convolutions; and, in the second place, an argument has been advanced with the view of showing that the pattern sketched out has, in all probability, a deep physiological significance.

Mr. Hill, in his masterly translation of Obersteiner's work, *On*

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24 "The Complete Fissures of the Human Cerebrum," *Journ. Anat. and Phys.*, vol. xxiv, 1890.

25 "Ein Fall von angeborenem Hydrocephalus internus," *Albert von Kölliker's Festschrift*, p. 307, Tafel xiii und xiv, 1887.

26 *Entwicklungsgeschichte des Menschen und der höheren Thiere*, 1879.

27 *Lehrbuch der Neurologie*, 1881.

the Anatomy of the Central Nervous Organs, gives expression to a similar opinion upon the functional value of the furrows and convolutions. He puts the matter in such an admirable manner that I feel constrained to quote the passage. He says: "No question in the comparative anatomy of the brain concerns the neurologist more closely than the question as to the morphological value of the fissures. Are they merely plaitings of a shifting surface, or are they boundaries of morphologically distinct organs? A study of the development of the fissures in the brains of animals which stand far apart in phylogeny teaches that they appear with such regularity as to sequence and progress in extension and obey such definite rules as to depth as would, in the case of other parts of the body, justify us in considering them as the divisions between structures of separate function."